The Genus *Caryota* in India

BY

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(*With two plates, seventy-five text-figures and a map*)

Introduction

The present paper is the 8th contribution to studies on palms undertaken by the senior author (T. S. M.) and his associates[1]. It deals with the genus *Caryota* in India. This genus is mainly concentrated in Indo-Malayan region having about 17 species of which 7 occur in India, 4 wild and 3 cultivated. The taxonomy of the genus is rather confusing due to the scarcity of authentic material and hybridization in cultivated plants.

Previous workers on it have been Linnaeus (1737), Griffith (1850), Seeman (1856), Bentham & Hooker (1883), Nicholson (1885), Drude (1887), J. D. Hooker (1892), Cooke (1908), Gatin (1912), Bailey (1914), Brandis (1921), Blatter (1926), McCurrach (1960), Tomlinson (1960 a, 1960 b, 1961, 1962) and Moore (1960, 1960 a). Moore (1960) has proposed a new taxon for the sub-family Caryotoideae in the classification of the Palmae.

Diagnostic features of the genus *Caryota*

The plants grow singly or in clumps, their stem being distinctly annulated. A jacket of adventitious roots surrounds the stem a little above the ground. The leaves are large and bipinnate, so uncommon in palms, the pinnae being borne on secondary axes of the leaf. Their vernation is induplicate. A single pinna is multicostate, divergent and strongly pulvinated. Stomata lie on both surfaces of the leaf and are characterised by ridges or teeth on the guard cells. In some species multi-cellular hairs are also present on the lower epidermis of leaf.

[1] For earlier contributions see T. S. Mahabale, & M. V. Parthasarathy, (1963) : *J. Bombay nat. Hist. Soc.* 60 (2) : 371.

The peduncles are very large and massive. They have a stout primary axis from which hang several horsetail-like secondary branches, forming a bunch of pendulous spikes. The inflorescences develop basipetally, i.e., from the apex down towards the base of the tree, and this is a unique habit of Caryotoid palms.

Each inflorescence is a spadix (Plate II, figs. 7, 8) encircled by 8-9 spathes enclosing about 40 secondary branches each bearing male and female flowers together. Generally they are in groups of three, the central flower being female and the laterals male. The male flowers develop and ripen earlier than the female. They drop off after pollination and fruits set in on the secondary branches in spikes. At maturity no male flowers are seen on them. The flowers have perianth with trimerous parts. In female flowers there are 1 or 2 hemi-anatropous or anatropous ovules and 3 staminodes. In male flowers the number of stamens ranges from 17-100. So far no pistillodes were observed in the male flowers.

Fruit is a 1- 2-seeded, non-fibrous drupe. The seed is ruminated, its surface being much corrugated. The conical embryo is lateral, and germination of the seed is '*Remotive*'. The first eophyll is simple, multicostate and convergent (Plate II, fig. 12).

Description of Species

A. *Wild Species*

1. **Caryota urens** L.

(Plate I, fig. 1)

This handsome species commonly known as *Bherli Mad* throughout Deccan or *Kitul* or 'Fishtail palm', attains a height of 12-22 m. in rain forests. It yields sago from its pith and commercial bristle fibre from the base of the leafstalk. The fibre being highly resistant to sea water is widely used for making fishing nets. Its outer bark is greyish brown in old trees and gets peeled off as periderm.

The crown of leaves is made up of 6-10 large bipinnately compound leaves measuring 4-4·5 m. The triangular leafbase is covered with fibres. Pinnae are borne on secondary axes. There is an odd terminal leaflet which provides a specific character. Each pinna has a pulvinus at the junction of the secondary axis of a leaf. The leaf being very large is often bent in the middle. There are 18-25

secondary rachises, each bearing 36 pairs of leaflets or pinnae in the basal part, 14 in the middle part and 5 in the apical part. They are arranged in a pyramidal manner.

Each leaflet or pinna is multicostate and divergent. There is no definite midrib but only 5-6 large costae.

A T.S. of the leaf at the point of attachment of pinna to rachis is 'V'-shaped. The vernation of entire leaf in *Caryota* is induplicate as in the *Sabaleae*. A developing leaf appears as a sword-like structure, its pinnae being closely folded together upon the secondary axis. Margins of the pinnae are connected to each other by thread-like ash-grey reins, held together by means of a pointed hook at the apex of leaf as in *Phoenix*. As the pinnae get separated from the apex, reins break off and hang downwards.

A single pinna is 30×4 cm., ashy green in colour and has shining surface. It is triangular in shape and thick in texture. There is a waxy coating on the abaxial face of the leaf.

The primary rachis ends in a bifid leaflet. Just below the terminal leaflet there are side pinnae below which lie two small pinnae, which are called here as the 'associated pinnae' to differentiate them from the side pinnae. The terminal leaflet is 22×8 cm., side pinnae 22×6 cm., and the associate pinnae 15×5 cm. There is also a terminal leaflet on the secondary axis, 23×40 cm. It also has side pinnae, 17×2·5 cm.

The inflorescence in this species is about 75 cm. long, completely enclosed within large boat-shaped spathes. The adult fruiting axis when out of spathe is 300-360 cm. in length, having a thick cylindrical primary axis with 40-42 secondary branches, the fruitiferous spikes (Text-fig. 53). They hang down in a thick cluster and hence the popular name, 'Horsetail palm'. The male flowers are 1·5 cm. long and sessile. They have two rudimentary bracts and 3 sepals each. The latter are imbricate, round and coriaceous and have frilled edges (Text-figs. 39-40). Petals 3, larger than sepals, pinkish, valvate. Stamens 40, acuminate, with short filaments. Anthers long and basi-fixed. Pollen grains are monocolpate, reticulate and 24×13·2 μ in diameter.

Female flowers, situated between two male flowers all along a spike have 2 scaly bracts and 3 ovate, concave and closely imbricate sepals (Text-fig. 41). Petals 3, round, ciliate and valvate, forming a persistent tube. Ovary superior, subtrigonal and has two anatropous ovules. Stigma sessile. There is a basal nectary. Fruit is a 2-seeded drupe, 1·3-1·4 cm. in diameter. The seeds have corrugated surface. Multicellular hairs are present on the seed coat.

Endosperm is ruminated. Its cells are porous. Epicarp is single-layered. A row of sclereides lies below the epicarp. The mesocarp is spongy and full of raphide sacs. Air cavities and tannin containing cells occur in it. The endocarp is generally few-layered. Seed coat is many-layered and full of tannin.

Germination of the seed is of the '*Remotive*' type. The first eophyll is simple, multicostate and convergent.

Habitat. Deciduous forests of Deccan, Konkan, Madras, Coimbatore, Central India, Orissa, evergreen forests of North Kanara, Malabar, Nilgiris, Sub-Himalayan regions, up to 2051 m. in Nepal. It is largely cultivated in gardens all over India, Middle East and elsewhere, often from unknown sources, for its beauty.

2. **Caryota rumphiana** Mart.

(Plate I, fig. 2)

This elegant palm 24-25 m. high is the tallest species of *Caryota* among those studied. Its single stem is distinctly annulate, with bark cracked into longitudinal slits. The towering crown of leaves is made up of 6-14 leaves, each measuring 5-6 m. The texture of pinnae is very thick and leathery compared to that in other species. The terminal leaflet of the primary axis of rachis is bifid. It measures 35×10 cm. The side pinnae are 32×5 cm. long. The terminal leaflet on the secondary rachis is 20×7 cm. and is without a tapering apex. The side pinnae are 17×7 cm.

The spadix is 12-14 cm. long and arises at right angles to the main axis of the tree, bearing about 45 pendulous spikes (Text-fig. 52). It is similar to that in *C. urens*, but the fruiting secondary axes are huge, 360-420 cm. long and are the largest among the inflorescences of species studied.

The male and female inflorescences are similar to those in *C. urens* and have long but thin perianth. The number of stamens in male flowers is 24. The fruit 1·6 cm. in diameter, is larger than that in *C. urens*. The epicarp consists of compactly arranged cells and 2-3 rows of sclereides. The mesocarp is multi-layered and has raphide sacs and tannin cells. The endocarp is papery and single-layered. The seed coat is filled with tannin. Surface of the seed is corrugated. The endosperm is ruminated, ruminations being heavily impregnated with tannin. Embryo is conical and lateral. Germination is of the '*Remotive*' type as in *C. urens*. Eophyll is simple, multi-costate and convergent.

A variety of this species grows in the Empress Gardens, Poona, which has 30 stamens instead of 24 in the male flowers and has highly ruminated seeds.

Habitat. This grows wild in Dandeli forests of North Kanara. It is cultivated in gardens, e.g., in J. J. School of Arts, Bombay, Empress Botanical Gardens, Poona, etc. It is found wild in Malay Archipelago, New Guinea, Borneo and North Australia.

3. **Caryota obtusa** Griff.

This palm has the same habit and stature as *C. urens*, but it can be recognised from it by the rounded, crenate apex of its leaflets. The male flowers are short and unexpanded. The number of stamens in male flowers is indefinite. It is a palm of high altitude.

Habitat. Wild in Upper Assam and Mishmi Hills, and is sometimes cultivated in gardens.

4. **Caryota sobolifera** Wall.

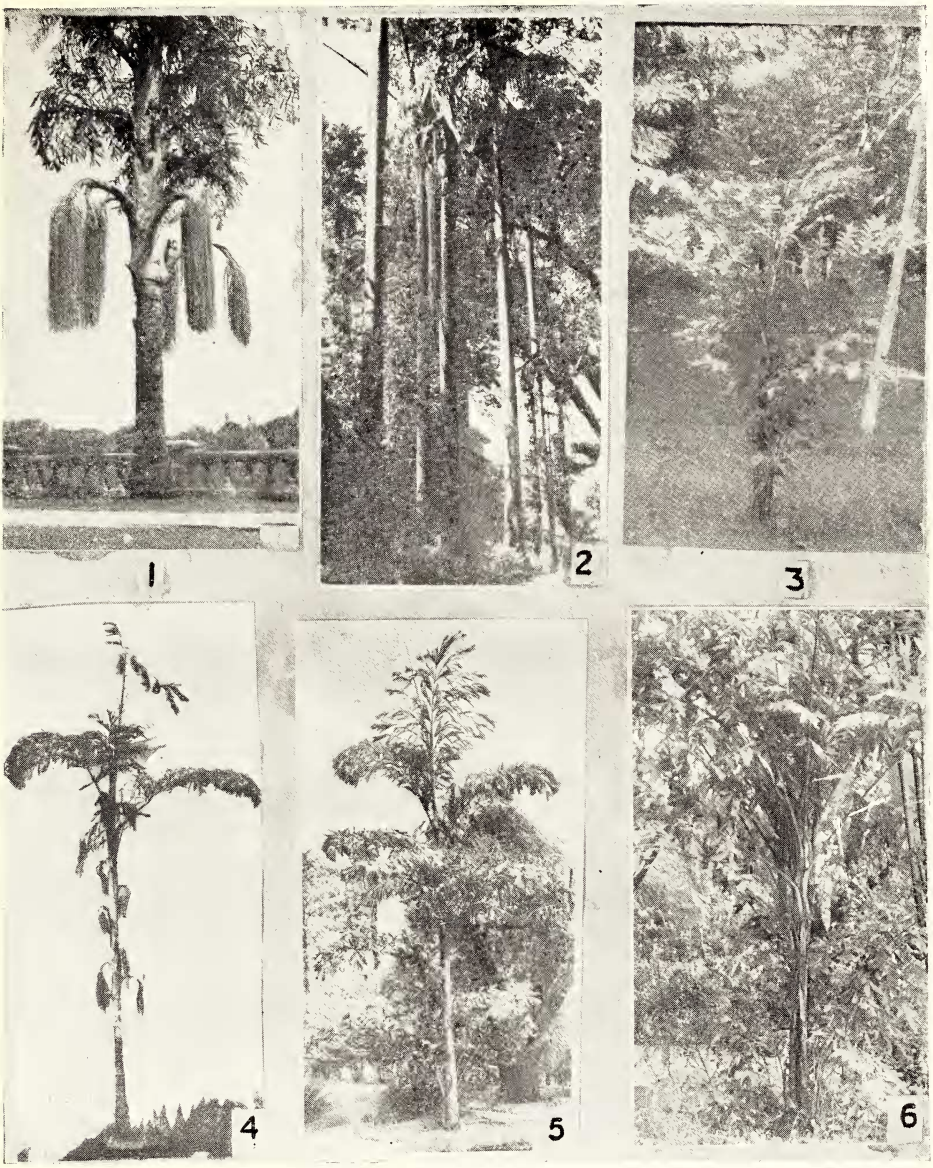
(Plate I, figs. 4, 5)

This is an ornamental species. It has one or two young shoots sprouting from below the base of the tree trunk, almost at ground level. Stem annulate. Adult plants attain a height of 10·5 m. The leaves are bipinnate, their crown being made up of 6-16 leaves. Each leaf is 2·1-2·4 m. long. The secondary axes bearing pinnae on a primary rachis of leaf are 14-25.

The number of pinnae is 5 in the apical region, 14 in the middle, and 36 in the basal region. A single pinna measures 10×2·5 cm. with 5 main costa ending in teeth.

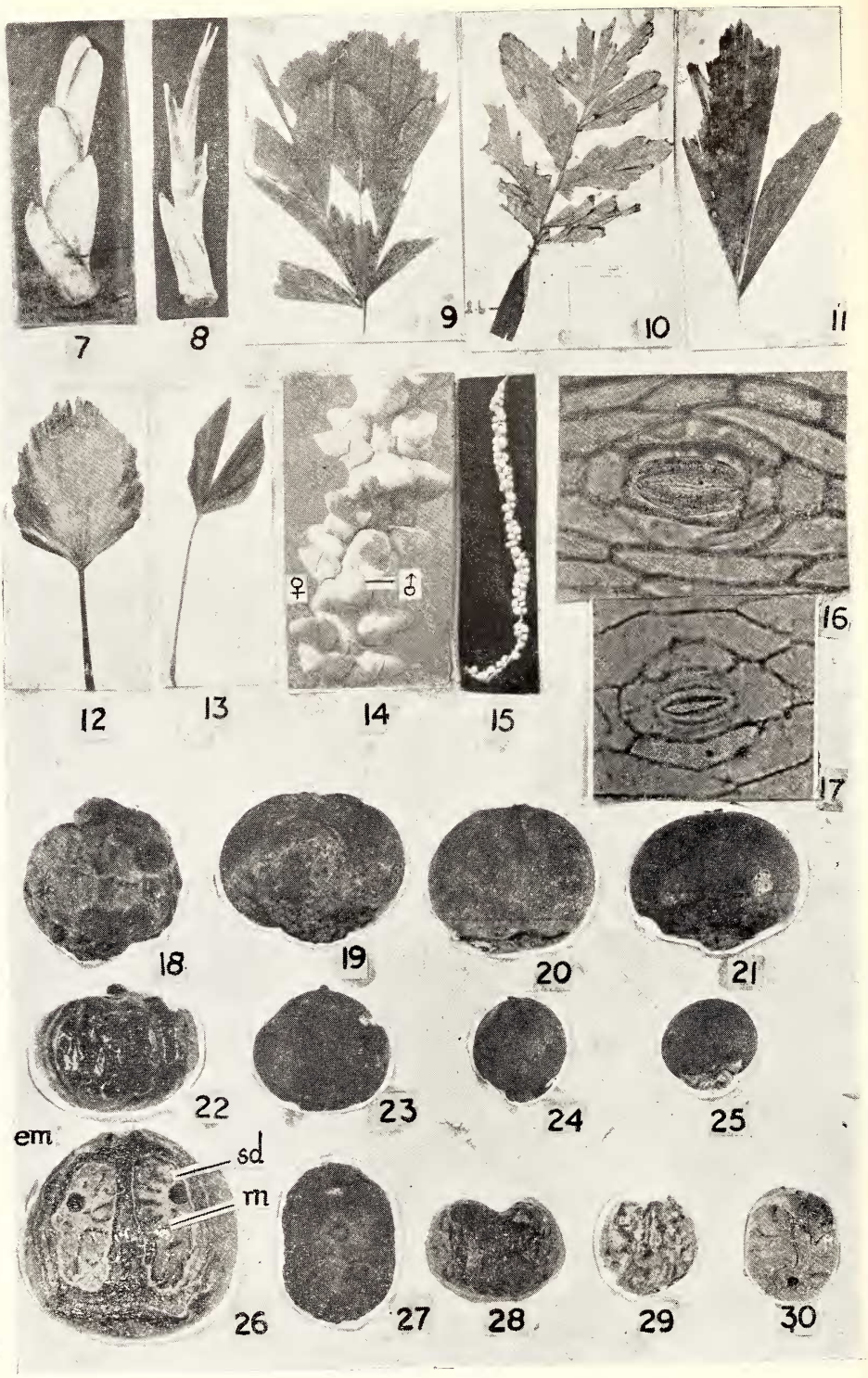
The terminal leaflet of the primary axis of a leaf measures 18·0× 14·0 cm. and has a deep incision. The side pinnae and the associated pinnae have central projection. Side pinnae are 18·0×6·0 cm. and the associated pinnae 9×3 cm. The terminal leaflet of the secondary axis is not tapering and is 17·0×18·0 cm. The associated pinnae measure 13·0×3·0 cm.

The inflorescences arise basipetally as in other species (Text-fig. 54), but the arrangement of flowers is quite different in this species. They lie in groups of two, one male by the side of one female flower at each juncture (Text-fig. 50). The male flowers are much curved in bud and have 2-3 staminodes each. Some hermaphrodite flowers are



Caryota species in India

1. *C. urens* L. (growing in Municipal Garden, Hyderabad), 2. *C. rumphiana* Mart. (growing in J. J. School of Arts, Bombay); 3. *C. plumosa* Hort. (growing in Royal Botanical Gardens, Peradeniya, Ceylon); 4 & 5. *C. sobolifera* Wall. (growing in B. Sahni Institute, Lucknow); 6. *C. mitis* Lour. (growing in Empress Botanical Gardens, Poona).



Morphology of leaf, inflorescence, fruit and seeds in *Caryota*

(For figure captions see page opposite)

also found in this species. The number of stamens per male flower is 17-21. The ovary is superior and bicarpellate.

Habitat. Upper Assam, Malaya; also cultivated in gardens, e.g., at the Birbal Sahni Institute of Paleobotany, Lucknow; Poona University Botanical Gardens, Poona etc.

B. *Introduced Species*

5. **Caryota mitis** Lour.

(Plate I, fig. 6)

This species is commonly grown in gardens for its bushy habit. New shoots arise from the axillary buds very close to earth from the base of the tree, or even from the portion a little below the ground. It attains a height of 7·5 m. The leaves are bipinnate, each pinna being without any long apical projection. Length of the leaf is 0·9-1·2 m. The leafbase is triangular. A pinna measures 17·0×5·0 cm. The terminal leaflet of the primary axis is 13·0×12·0 cm. with two side pinnae. The number of pairs of pinnae on the secondary axes of leaf is 5 in the apical region, 4 in the middle region and 6 in the basal region. The terminal leaflet of a secondary axis is 20·0×8·5 cm. and has tapering apex. The associated pinnae are 11×5 cm.

The inflorescences are intrafoliar and arise basipetally. They arise even at the lowest node of the tree trunk at the ground level. The spadix has a beak-shaped apex and 8 spathes. It bears about 30 spikes (Text-fig. 51). The arrangement of male and female flowers here is the same as in *C. urens.*

Morphology of leaf, inflorescence, fruit and seeds in Caryota.

7, 8. Spadix in *C. mitis* and *C. urens* respectively. 9. *C. sobolifera.* Terminal leaflet of the primary axis of leaf. 10. *C. mitis* Adult leaf. Note the leaf base-*lb.* 11. *C. plumosa.* Terminal leaflet of the primary axis of leaf. 12. *C. urens.* Simple eophyll x *c.*½. 13. *C. urens.* A bifid eophyll x *c.* ½. 14. *C. urens.* Arrangement of flowers on a secondary axis of inflorescence showing ♂ and ♀ flowers x *c.* ½. 15. *C. urens.* Secondary axis of inflorescence showing crowded fruits. 16. *C. urens.* A stoma on the lower epidermis x *c.* 340 : Note the cuticular bands-*cb* on the guard cells. 17. *C. mitis.* A stoma on the lower epidermis x *c.* 340 : Note wavy walls of cells and cuticular bands on the guard cells. 18-23 Fruits in *C. maxima, C. rumphiana, C. obtusa, C. urens, C. cumingii, C. plumosa* x *c.*½. 24-25. *C. mitis* x *c.* ½. 26. *C. urens* L. S. of a fruit showing seed—*sd,* ruminations—*rn* and lateral position of embryo—*em* x *c.* 3. 27-28. *C. urens.* Seeds : Note the corrugated surface in 27 and lobed structure in 28. 29. *C. plumosa.* Seed x *c.* 4. 30. *C. mitis.* Seed x *c.* 4 : Note the ruminations.

Male flowers have two scaly rudimentary bracts and 3 sepals with ciliated margin (Text-fig. 42). Petals 3, reddish and conical. Stamens 17. Anthers as long as the petals, basifixed. Female flowers develop after the male flowers. They have 3 filamentous staminodes as in *C. urens* (Text-fig. 49). The fruit is a one-seeded drupe 0·5 cm. in diameter. The seed coat is much corrugated.

Ectocarp layer of the fruit is limited by a row of sclereides. The mesocarp is similar to that in *C. urens*. Endocarp is single-layered, unlike the many-layered endocarp of *Hyphaene*, *Cocos*, etc. The ruminations extend to the interior of the endosperm. They have thick lamellae full of hemicellulose. The embryo is conical and lateral. The seeds do not readily germinate. New plants are easily obtained from suckers as in *C. sobolifera*. The eophyll is simple and has convergent venation.

Habitat. Burma, from Arakan southwards, Martaban. Malay peninsula, Penang. Andaman Islands. Often cultivated in gardens in India.

6. **Caryota plumosa** Hort.

(Plate I, fig. 3)

The tree attains a height of 7 m. Its plumose leaves are highly characteristic. The feathery nature of leaves is due to close insertion of very thin pinnae on the rachis, opposite to each other. The stem is distinctly annulate and woody.

The crown of leaves has about 20 bipinnate leaves, each measuring 1 m. There are 2-18 secondary axes on each leaf, 5 pairs in the apical part, 4 in the middle and 8 in the basal. At each node there are two pinnae, one small and the other large, 5·0×1·0 cm. and 10·0×2·6 cm. respectively.

The terminal leaflet of the primary axis of the leaf, 20×8·5 cm., is tapering. The side pinnae are 11×5 cm.

The inflorescence has a few pendulous spikes, 20-30 per fruiting axis. The arrangement of flowers is similar to that in *C. mitis*. There are 17 stamens in a male flower. The fruit is one-seeded drupe, seed coat wrinkled and endosperm filled almost completely by ruminations. This character of the seed of this species is so distinct and different, that it forms a diagnostic feature of this species.

The percentage of germination of seeds in this species is very low. New plants arise mostly by suckers. The first eophyll is simple, multicostate and convergent.

Habitat. This species is originally from Brazil and has been introduced in India and Ceylon. It grows well in Peradeniya Gardens, Ceylon.

7. **Caryota cumingii** Lood.

The single-stemmed tree reaches a height of 13·5 m. The spathes and peduncles are massive. The rings on the tree trunk are very deep and resemble steps. The fruit is a drupe, 1·4 cm. in length. Seeds take about a year to germinate.

Habitat. A native of Philippine Islands. Sometimes introduced in gardens elsewhere, e.g., in the Fairchild Tropical Garden, Florida, U.S.A. It is the rarest species grown in India.

General Considerations

A. *Morphological*

(1) Stem: The stem in palms though generally single and soboliferous, shows several types. Van Mohl (1845) has proposed a classification of palms on the basis of stem characters: (a) *Geonoma*-like, (b) *Calamus*-like, (c) *Mauritea*-like, (d) *Cocos*-like and (e) the so-called stemless palms like *Nipa*. A considerable amount of food material accumulates in the trunk and it takes different shapes.

The stem of *Caryota* is *Cocos*-like. It is cylindrical, woody and distinctly annulate, the number of annuli varying from 15-25, and internodes from 13-45 cm. The young stem is covered with woolly tomentum in *C. plumosa* and *C. mitis.*

The growth habit of *Caryota* stem is of two kinds: single and soboliferous as in *C. urens*, and clumpy with several reedy stems as in *C. mitis.* In *C. sobolifera* one or two shoots arise from the main soboliferous trunk near its base, but not many as in *C. mitis.* One can easily recognise different species with the help of stem characters: —

I. Plants growing singly, stem annulate, internodes long, surface of the tree trunk rough and with vertical cracks :

Trees 12 m. high, the length of an internode 40 cm..... *C. urens* (Text-fig. 1).

Tree 24 m. high, internodes more than 40 cm. long, bark very hard..... ..... *C. rumphiana* (Text-fig. 2).

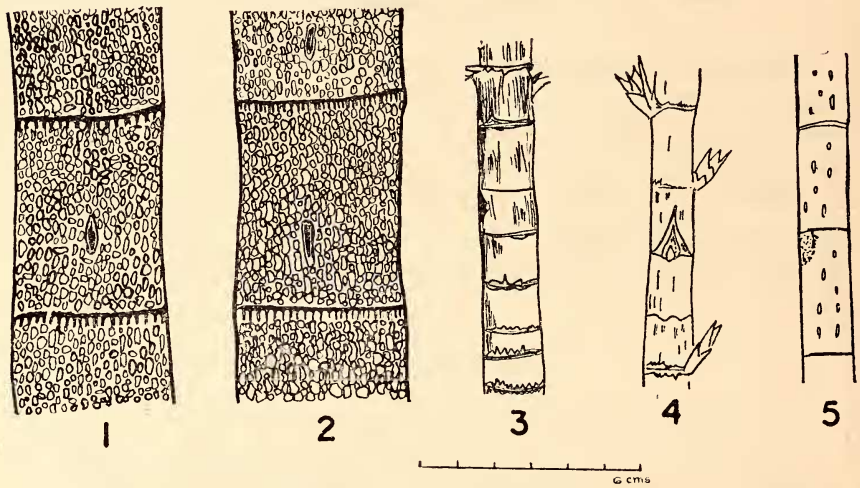
Trees 13·4 m. high, with deep nodal depressions..... *C. cumingii.*

II. Plants growing in clumps, internodes small, bark smooth but clothed with woolly tomentum when young. Scars of fallen leaf-bases and peduncles at nodes prominent :

Trees 7 m. high, internodes 18 cm. long, nodes very conspicuous, bark woody ..... *C. plumosa* (Text-fig. 5).

Trees 10-11 m. high, stem soboliferous with one or two basal shoots, internodes 25 cm. long..... *C. sobolifera* (Text-fig. 3).

Trees 6-7 m. high, length of an internode 13 cm., stem clothed with woolly tomentum when young..... *C. mitis* (Text-fig. 4).



Figs. 1-5. Stem in *Caryota*

Fig. 1. *C. urens* ; Fig. 2. *C. rumphiana* ; Fig. 3. *C. sobolifera*; Fig. 4. *C. mitis*; Fig. 5. *C. plumosa*

(2) Roots and Rooting Region: The basal portion of the tree trunk a little above and below the ground gives rise to many adventitious roots, which cover one or two nodes above the ground. They are relatively few and thick, often not fully developed, swollen and twisted. They dry up and die and are not absorbing. In *C. rumphiana* and *C. urens* they occupy 2-4 annuli above the ground and 2-3 below it. Those below the ground growing laterally function as stilt roots. The other underground ones are extensive and form a bowl-shaped root-bearing base from which the roots radiate in all directions over a long distance. For example, in *C. rumphiana* they extend to 8 m. from base.

(3) Leaf: The leaf in *Caryota* is quite different from that in other palms because (i) of its bipinnate nature, (ii) induplicate vernation of leaflets, (iii) absence of mid-vein, (iv) swollen pulvini at the base of the leaflets on the secondary axes, (v) fan-shaped lamina with multicostate divergent veins, and (vi) the presence of odd

terminal leaflet at the apex of the primary and secondary rachises. The odd terminal leaflet forms a diagnostic character of species. It has two side pinnae just below the terminal leaflet and two small triangular associated pinnae in some species e.g. in *C. urens*, *C. sobolifera* and *C. mitis*. The associated pinnae are just below the side pinnae in *C. urens* and *C. mitis* or in between the terminal pinnae and the side pinnae in *C. sobolifera*.

The leafbase is long, ligulate and more or less tubular. In related palms such as *Areca* it is not tubular. The leaf sheath splits ventrally and is connected to the main trunk by persistent fibres highly resistant to decay.

It may be noted here that multicostate divergent venation of leaflets as in *Caryota* is also found in other members of the Caryotoideae such as *Wallichia*, *Arenga* and *Didymosperma* and in some *Cocoineae* like *Martinezia*. But the leaflets of *Martinezia* have a distinct midrib which is wanting in *Caryota*. Induplicate vernation also is seen in tribes Coryphoideae, Phoenicoideae, Borassoideae, but in Coryphoideae the pinnae have no midrib.

All these leaf characters are useful in identification of species (see Table p. 472):—

I. Terminal leaflet of the primary rachis with a deep incision :

Terminal leaflet with a pair of side pinnae and two associated pinnae below the side pinnae..... *C. urens* (Text-fig. 6).

Terminal leaflet 17×7 cm., with a deep incision, four associated pinnae lying between the terminal and side pinnae..... ..... *C. sobolifera* (Plate II, fig. 9 and Text-fig. 10).

Terminal leaflet 13×12 cm., associated pinnae two, side pinnae with central projection..... *C. mitis* (Plate II, fig. 10 and Text-fig. 9).

II. Terminal leaflet of the primary rachis without a deep incision :

Terminal leaflet thick and leathery, 35·6×10 cm., associated pinnae absent, side pinnae present below the terminal leaflet.... *C. rumphiana* (Text-fig. 7).

Terminal leaflet thin and papery, without a deep incision, 17×7 cm., side pinnae generally one, and without any associated pinnae..... ..... *C. plumosa* (Plate II, fig. 11 and Text-fig. 8).

(4) Stomata: The stomata in the Caryotoideae have a unique character namely, teeth on the guard cells, which forms an important character of the Caryotoid palms. However, it has been reported in *Bactris* not belonging to Caryotoid palms (Tomlinson 1961), and in *Equisetum* unrelated to palms.

Epidermal cells of the leaf are either smooth as in *C. urens*, *C. rumphiana* (Plate II, fig. 16; Text-fig. 22), or wavy as in *C. mitis*

TABLE

MORPHOLOGY OF STEM, LEAF, STOMATA, INFLORESCENCE, FLOWERS, FRUIT AND SEED IN *Caryota*

	C. urens 1	*C. rumphiana* 2	*C. plumosa* 3	*C. sobolifera* 4	*C. mitis* 5
STEM	Single 12-19 m. with 15-20 annuli	Single 24-38 m. with 20 annuli	In clumps 7 m. with less than 15 annuli	Generally 2, 10.5 m. with less than 15 annuli	More than 5, each 7 m. with less than 20 annuli
LEAVES :	3·9-4·5 m. long.	5·1-6·0 m.	1·0-1·5 m.	2·1-2·4 m.	0·9-1·2 m.
Pinnae	30×4 cm.	35×4 cm.	10×2·5 cm.	16×4 cm.	17×5 cm.
Texture	Leathery with waxy coating	Very leathery	Very thin	Not thick	Very thin
Terminal leaflet of the primary rachis	22×8 cm., bifid, with a long central projection	35·0×10·0 cm., bifid	17·0×7 cm., incision deep	18×14 cm., incision deep	13·0×12·0 cm., incision deep
Associated pinnae-length and breadth	15×5 cm.	32×5 cm.	24×3·5 cm.	18×6 cm.	17×5 cm.
Number of secondary axes on the primary petiole or rachis	18-25	20-25	10-20	14-25	12-18
Number of pinnae per secondary axis	14	14	4	4-6	4
Terminal leaflet of the secondary axis	23×40 cm., with one end pointed	20×7 cm., with end not pointed	12×3 cm., with end not pointed	17×8 cm., with end not tapering	20×8.5 cm., with one end tapering

	1	2	3	4	5
Associated side pinnae	17×2·5 cm.	18×7 cm.	15×3 cm.	13×3 cm.	11×5 cm.
EPIDERMIS AND STOMATA :					
Epidermal cells	Straight-walled	Straight-walled	Wavy-walled, hairs present on lower epidermis	Wavy-walled	Wavy-walled, epidermal hairs on lower surface
Stomata on the guard cells	40×20 μ, with 14-16 cuticular bands	51×21 μ, with 16-18 cuticular bands	22×13 μ, with 14-16 cuticular bands	15×8 μ, with 14-16 cuticular bands	22×13 μ, with 8-9 cuticular bands
INFLORESCENCE :	300-360 cm., spikes 40 per spadix	360-420 cm., spikes 40-46	40 cm., spikes 25-30	37 cm., spikes 35	30 cm., spikes 30
A spike on secondary axis	150 cm., long	150 cm.	30 cm.	30 cm.	30 cm.
FLOWERS :					
Stigma in ♀ flowers	Sessile, 2-3-fid, ovules 2 anatropous	Sessile, 2-3-fid, ovules 2 anatropous	Sessile, 2-3-fid, ovules 2 anatropous	Sessile, 2-fid, ovule 1, hemi-anatropous	Sessile 1, ovule 1, hemi-anatropous
Staminodes in ♂ flowers	0	0	1-3	0	0
Pollen grains	24·0×13·2 μ	21·6×6·4 μ	13·2×11·6 μ	13·6×11·6 μ	13·1×11·5 μ
FRUIT :					
Diameter	1·4 cm.	1·6 cm.	—	0·7 cm.	0·5 cm.
SEEDS:	2, 1·2 cm. in diameter	2, 1·4 cm. in diameter	—	1, 0·4 cm. in diameter	1, 0·5 cm. in diameter

TABLE

MORPHOLOGY OF STEM, LEAF, STOMATA, INFLORESCENCE, FLOWERS, FRUIT AND SEED IN *Caryota*

	C. urens 1	*C. rumphiana* 2	*C. plumosa* 3	*C. sobolifera* 4	*C. mitis* 5
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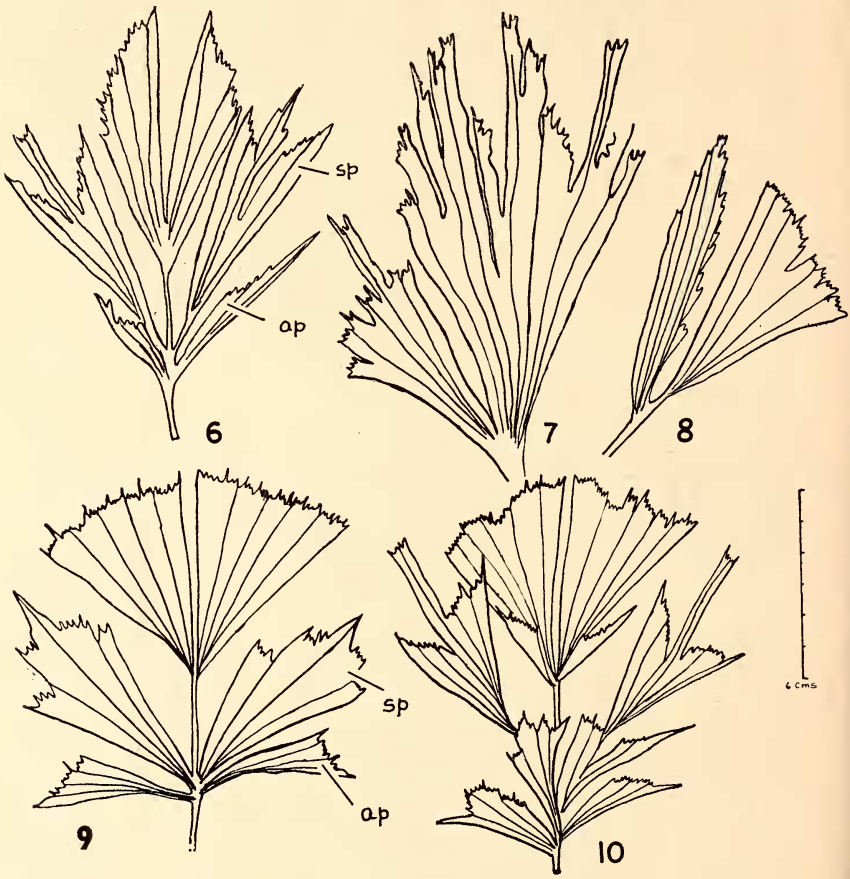
LEAVES :	3·9-4·5 m. long.	5·1-6·0 m.	1·0-1·5 m.	2·1-2·4 m.	0·9-1·2 m.
Pinnae	30×4 cm.	35×4 cm.	10×2·5 cm.	16×4 cm.	17×5 cm.
Texture	Leathery with waxy coating	Very leathery	Very thin	Not thick	Very thin
Terminal leaflet of the primary rachis	22×8 cm., bifid, with a long central projection	35·0×10·0 cm., bifid	17·0×7 cm., incision deep	18×14 cm., incision deep	13·0×12·0 cm., incision deep
Associated pinnae-length and breadth	15×5 cm.	32×5 cm.	24×3·5 cm.	18×6 cm.	17×5 cm.
Number of secondary axes on the primary petiole or rachis	18-25	20-25	10-20	14-25	12-18
Number of pinnae per secondary axis	14	14	4	4-6	4
Terminal leaflet of the secondary axis	23×40 cm., with one end pointed	20×7 cm., with end not pointed	12×3 cm., with end not pointed	17×8 cm., with end not tapering	20×8.5 cm., with one end tapering
	1	2	3	4	5
Associated side pinnae	17×2·5 cm.	18×7 cm.	15×3 cm.	13×3 cm.	11×5 cm.
EPIDERMIS AND STOMATA : Epidermal cells	Straight-walled	Straight-walled	Wavy-walled, hairs present on lower epidermis	Wavy-walled	Wavy-walled, epidermal hairs on lower surface
Stomata on the guard cells	40×20 μ, with 14-16 cuticular bands	51×21 μ, with 16-18 cuticular bands	22×13 μ, with 14-16 cuticular bands	15×8 μ, with 14-16 cuticular bands	22×13 μ, with 8-9 cuticular bands
INFLORESCENCE :	300-360 cm., spikes 40 per spadix	360-420 cm., spikes 40-46	40 cm., spikes 25-30	37 cm., spikes 35	30 cm., spikes 30
A spike on secondary axis	150 cm., long	150 cm.	30 cm.	30 cm.	30 cm.
FLOWERS : Stigma in ♀ flowers	Sessile, 2-3-fid, ovules 2 anatropous	Sessile, 2-3-fid, ovules 2 anatropous	Sessile, 2-3-fid, ovules 2 anatropous	Sessile, 2-fid, ovule 1, hemi-anatropous	Sessile 1, ovule 1, hemi-anatropous
Staminodes in ♂ flowers	0	0	1-3	0	0
Pollen grains	24·0×13·2 μ	21·6×6·4 μ	13·2×11·6 μ	13·6×11·6 μ	13·1×11·5 μ
FRUIT : Diameter	1·4 cm.	1·6 cm.	—	0·7 cm.	0·5 cm.
SEEDS:	2, 1·2 cm. in diameter	2, 1·4 cm. in diameter	—	1, 0·4 cm. in diameter	1, 0·5 cm. in diameter

(Plate II, fig. 17). The distribution of stomata is more on the lower epidermis than on the upper. Persistent multicellular bases of hairs are seen on the lower epidermis of leaf in *C. mitis* and *C. plumosa.*

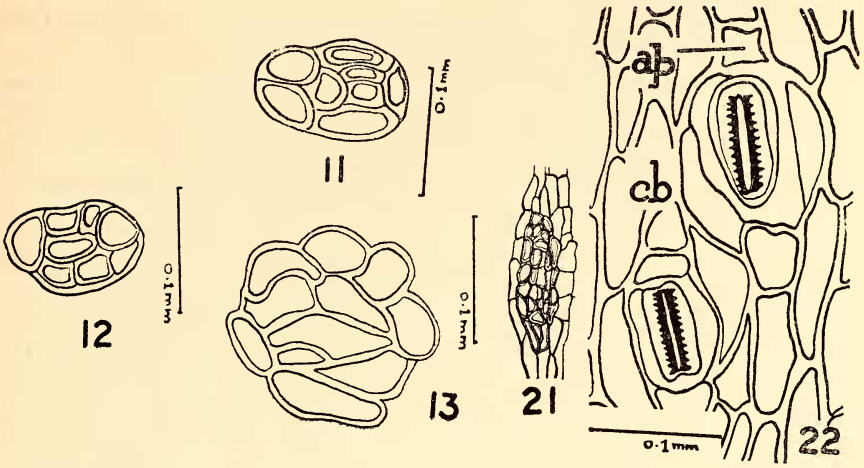


Figs. 6-10. Terminal leaflets

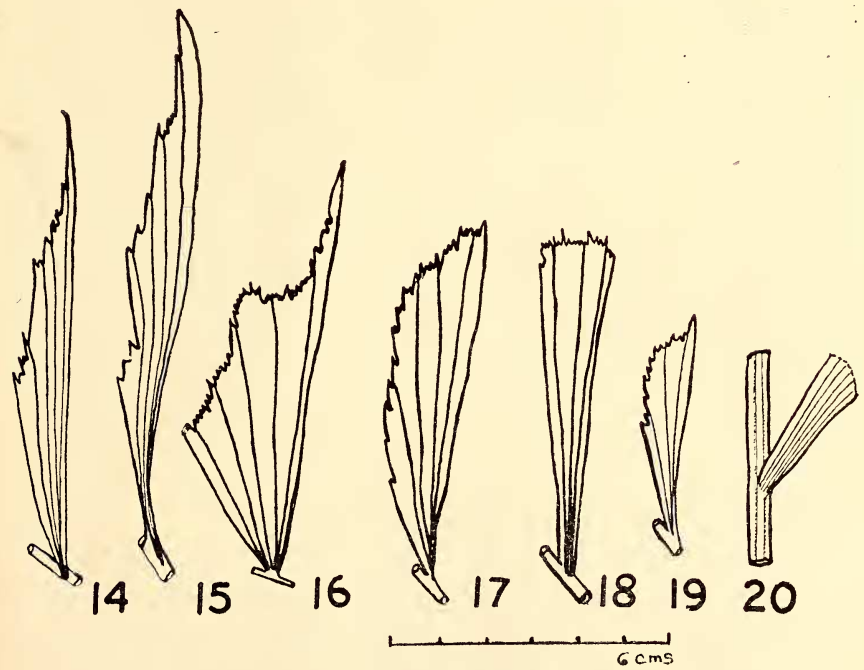
Fig. 6. *C. urens*; Fig. 7. *C. rumphiana*; Fig. 8. *C. plumosa*; Fig. 9. *C. mitis*; Note the side pinnae—*sp*, and the associated pinnae—*ap*. Fig. 10. *C. sobolifera*

Similar hair bases are present in the intercostal region of the leaves in *Wallichia disticha* and *Arenga saccharifera* (Text-figs. 13, 11).

(5) Leaf form: These are shown in Plate II, figs. 9-13. Brown (1956) reported some leaves of palms from the Middle and Upper Triassic of Colorado under the name *Sanmiguelia.* This is an important discovery though controversial, as it extended the ancestry of angiosperms far too back. Angiosperms are generally believed to have arisen mainly in the Cretaceous period. Assuming *Sanmiguelia* to be a palm and not an outsized *Ginkgo* or *Cordaites*, or a large *Schizoneura* as has been thought, it certainly helps us



Figs. 11-13 & 21. Bases of hairs on the lower epidermis in *Arenga saccharifera*, *C. plumosa*, *Wallichia disticha*, and *C. mitis* respectively. Fig. 22. *C. rumphiana*. Stoma on the lower epidermis. Note the cuticular bands on the guard cells *cb*, the apical cells (pole cells)—*ap*.



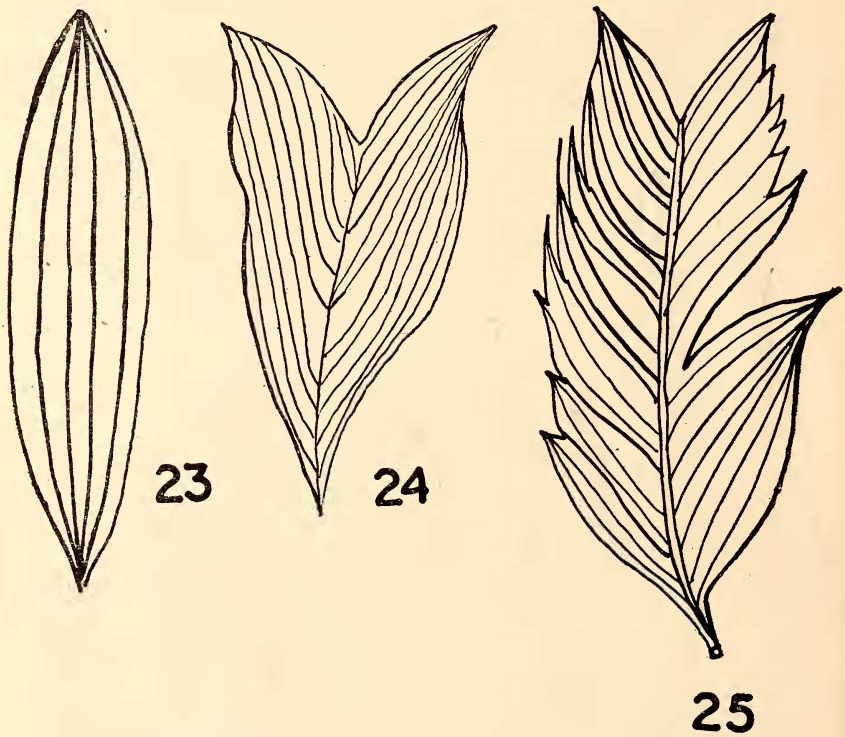
Figs. 14-20. Pinna

Fig. 14. *C. urens*; Fig. 15. *C. rumphiana*; Fig. 16. *C. mitis*; Fig. 17. *C. sobolifera*; Figs. 18, 19. *C. plumosa*; Fig. 20. *C. plumosa*. Attachment of pinna

in tracing the origin of the pinnate versus palmate habit of leaves in palms, as the leaves in *Caryota* are intermediate in form, and have multicostate convergent or divergent veins as in *Sanmiguelia.*

The leaves in *Caryota* are bipinnate, a condition so rarely found in palms. The pinnae are cuneate, multicostate and divergent, neither pinnate as in *Cocos* or *Phoenix*, nor palmate as in *Borassus.* The question, therefore, arises as to how these two dominant forms of leaves in palms have arisen?

Ontogeny of leaf in palm throws some light on this question. Both these dominant types of leaves can be derived from a common source such as multicostate simple leaf in young *Caryota.* Eophylls in *Cocos nucifera, Hyphaene indica, Phoenix acaulis, Livistona chinensis,* and the transitional leaf forms in other palms have entire lamina with multicostate convergent venation (Tomlinson 1960 a).



Figs. 23-25. *Cocos nucifera.* Seedling leaves

In palmately cut leaves of *Livistona* also the eophylls are entire, but they get split later at the apex repeatedly above the ligule, so that veins seem to arise from a single ligule on the petiole. Thus the initially convergent veins of an eophyll become divergent, the

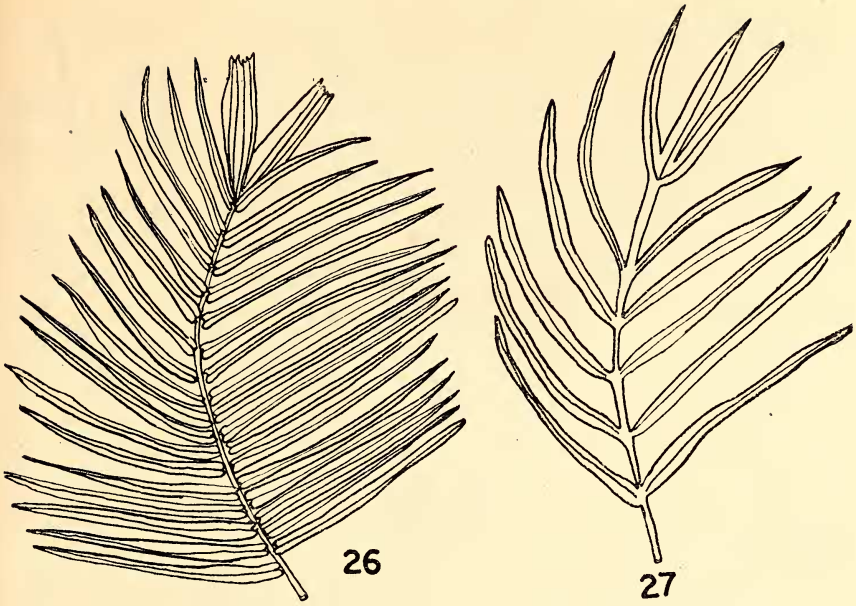
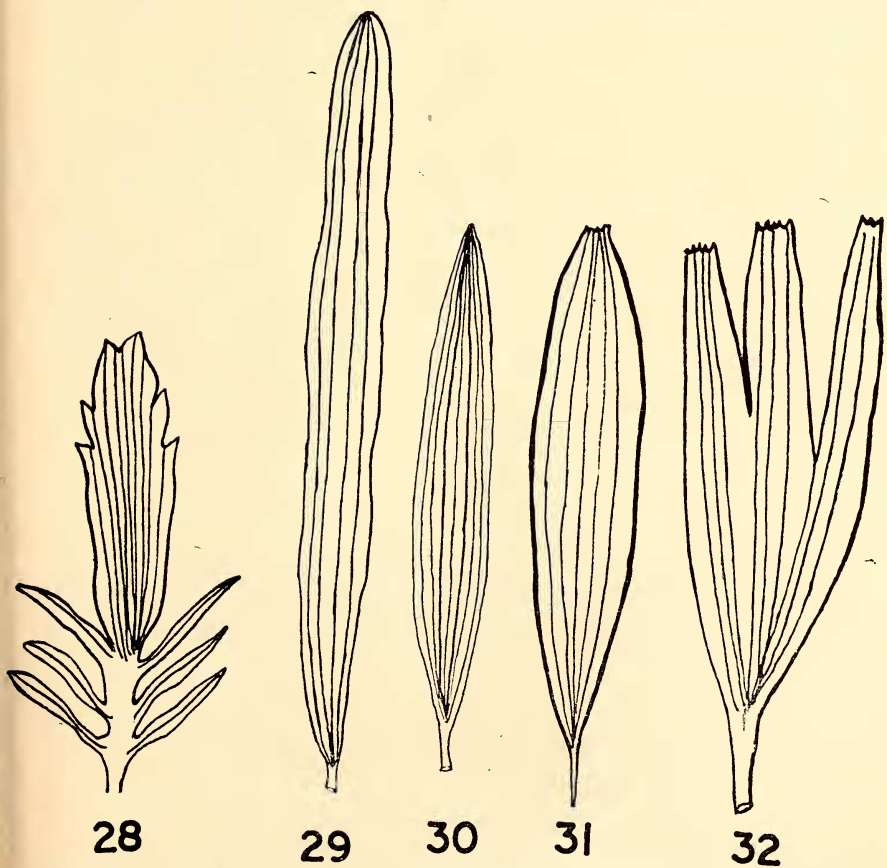


Fig. 26. *Cocos nucifera.* An adult leaf (diagrammatic)
Fig. 27. *Phoenix acaulis.* An adult leaf (diagrammatic)



Figs. 28, 30. *Phoenix acaulis.* Early eophylls. Fig. 29. *Hyphaene indica.* Eophyll
Fig. 31. *Livistona chinensis.* An eophyll. Fig. 32. *L. chinensis.* A trifid eophyll

veins being inserted on the ligule divergently and not one above the other as in the pinnatisect leaves (*cf.* Text-figs. 28, 30, 31 & 32).

In pinnate type of leaf as in *Phoenix*, the first eophyll is simple with convergent veins but the basal pinnae get separated first, the pinnae above unfolding acropetally and not simultaneously.

The early eophylls in *Caryota* are entire, multicostate and convergent (Plate II, fig. 12). As the pinnation starts, the eophyll becomes bifid. With further pinnation of the first order, divergence of the costa increases and a fan-shaped leaf is formed. After a couple of pinnae are formed, secondary rachises arise on the primary rachis of leaf and pairs of pinnae begin to appear on the secondary rachises. Ultimately a bipinnate leaf results, with a terminal odd leaflet. In adult leaf young pinnae on secondary rachises are held together by thin reins before unfolding. The splitting of the pinnae starts as in palmate palms and the reins hang down from the margin as in several palms (Eames 1953).

At maturity each pinna in *Caryota* shows multicostate divergent venation like that in an adult leaf of a palmate palm, but the arrangement of pinnae and the entire leaf are more like those in a pinnate leaf. It, therefore, seems to represent an intermediate type of leaf

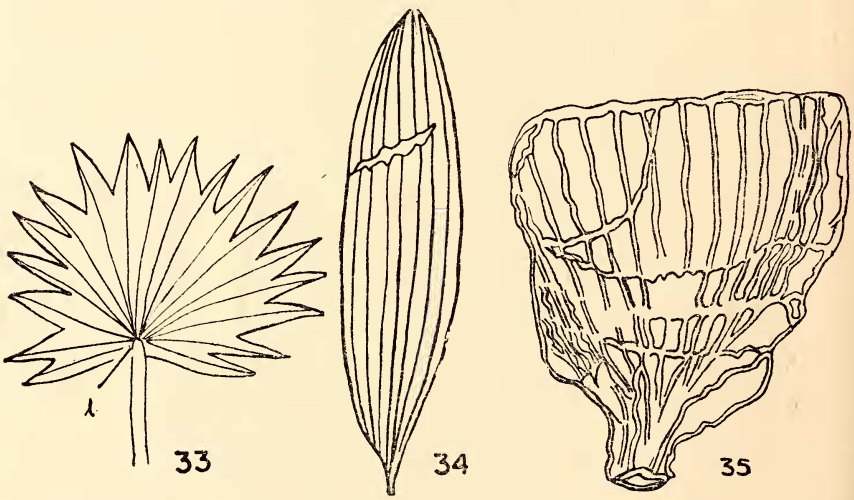


Fig. 33. *Livistona chinensis*. An adult palmate leaf (diagrammatic). Note the ligule—l at which the cut pinnae remain united without getting separated from each other; Fig. 34. *Sanmiguelia lewisi*. A simple leaf showing convergent costa (after Brown 1956); Fig. 35. *Sanmiguelia lewisi*. A multicostate-leaf (possibly, divergent) (after Brown 1956)

between the two well known patterns of palm leaves, both of which can be derived from a common simple multicostate, ribbed convergent leaf like the eophylls of *Caryota*.

The leaf in *Sanmiguelia*, if it be a real palm, which we believe it is, assumes greater significance in this context, as it shows how *Caryota* leaves could have been derived. *Sanmiguelia* has simple, multicostate, convergent or divergent leaf as in *Caryota*. Its shape is similar to that in the eophylls of palms, which later on gives rise to pinnate or palmate leaves (see diagram p. 480). Should this be really so, the shape of adult leaf in *Caryota* seems to represent a very ancient type of palm leaf, similar to that in *Sanmiguelia*, and suggests that palm leaf may have been evolved as shown below:—

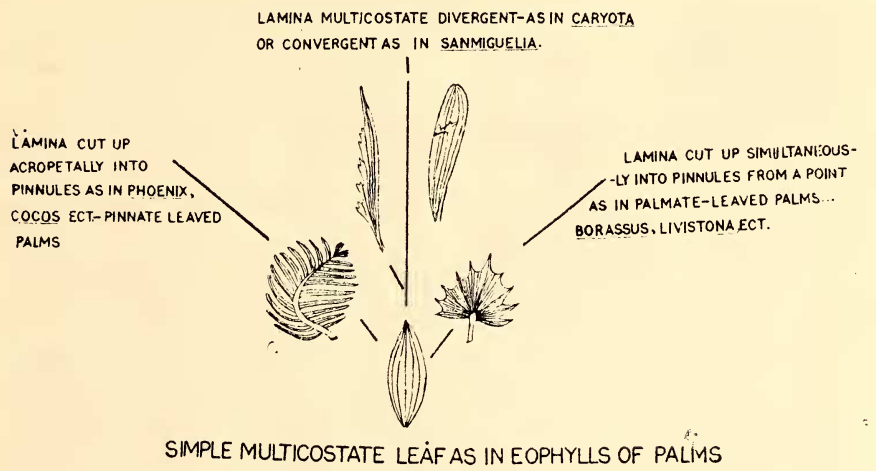


Diagram illustrating the phylogeny of palm leaves

(6) Inflorescence and flowers: (Plate II, figs. 7, 8, 14; Text-figs. 39-54)

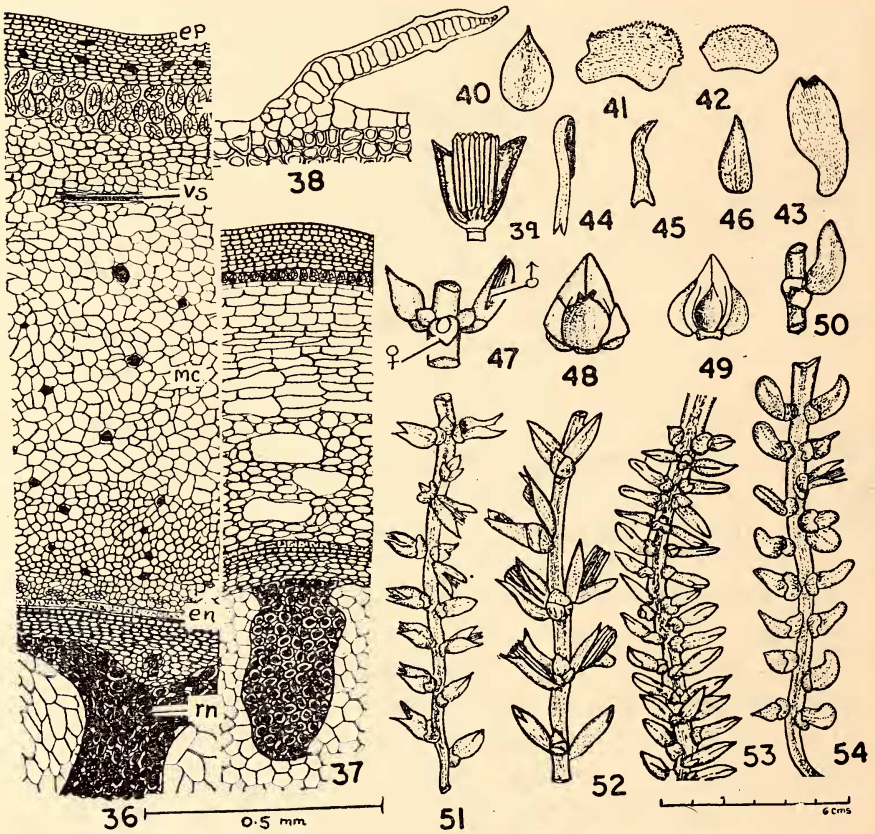
The inflorescences in *Caryota* are highly characteristic because they arise basipetally. In extreme cases as in *C. mitis* they arise even at the ground level and then the plant dies. But new suckers propagate the species vegetatively.

The flowers in *Caryota* are unisexual. In male flowers in *C. sobolifera*, there are 1-3 large staminodes. A few hermaphrodite flowers are also seen in this species. The number of stamens forms a distinguishing character for specific identification. In the female flower the ovary is subtrigonal, mono- or bicarpellary. The stigma is sessile and bi- or trifid. Three filamentous staminodes are present in female flowers, but there are no pistillodes in male flowers (Text-figs. 43-46 and 48, 49).

(7) Fruit and Seeds: (Plate II, figs. 15, 18-30; Text-figs. 36-38, 55-60)

The fruit in *Caryota* is 1-2 seeded drupe, two-seeded in *C. urens* and *C. sobolifera* and one-seeded in *C. mitis* and *C. plumosa.* The largest fruit is that of *C. maxima* which is 1·4 cm. in diameter as against 1·2 cm. of *C. urens* or 0·4 cm. in *C. mitis.*

The seed in *Caryota* is endospermous and highly wrinkled outside with grooves and furrows. The endosperm is ruminated and forms another diagnostic feature of the genus. The extent of rumination



Figs. 36-54. Inflorescence, flower, fruit and seeds in *Caryota*

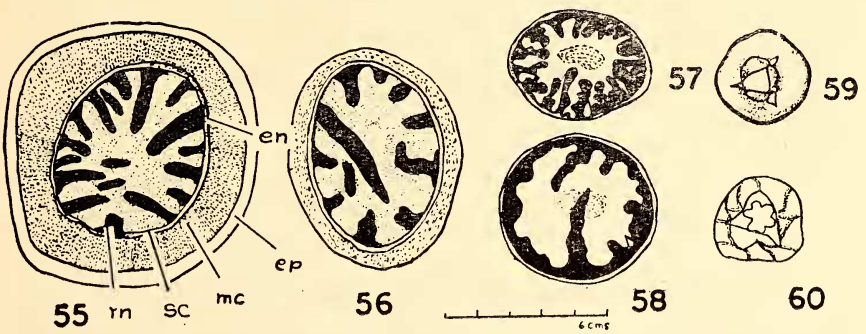
Figs. 36, 37. *C. urens, C. mitis,* T.S. of fruit showing epicarp—*ep,* mesocarp—*mc,* vascular trace—*vs,* endocarp—*en,* ruminations—*rn,* Fig. 38. *C. urens.* A seed hair. Fig. 39. *C. urens.* Male Flower. Fig. 40. *C. urens.* Sepal of a male flower. Fig. 41. *C. urens.* A sepal of a female flower showing frilled edge. Fig. 42. *C. mitis.* Sepal of a male flower. Figs. 43, 44, 45, 46. *C. sobolifera.* Staminodes in a male flower. Fig. 47. *C. urens.* Arrangement of flowers showing one female between two male flowers. Figs. 48, 49. *C. urens* and *C. mitis.* A female flower showing ovary and filamentous staminodes. Fig. 50. *C. sobolifera.* One male and one female flower side by side. Fig. 51. *C. mitis.* Fig. 52. *C. rumphiana.* Fig. 53. *C. urens.* Fig. 54. *C. sobolifera.* Secondary axis of inflorescence

differs in different species. In *C. plumosa* the ruminations are many, extending up to the central part of the seed, but in *C. urens* they are not so extensive.

The seed coat is multi-layered. In germination multicellular hairs develop on its surface. Other details regarding the seed are given in the Table (pp. 472-73). The endosperm cells are 159×36 μ in *C. urens*, 226×80 μ in *C. rumphiana*, 80×25 μ in *C. mitis* and 75×22 μ in *C. plumosa*.

(8) Germination: (Text-figs. 61-75)

The seeds of *C. urens* and *C. rumphiana* germinate in about 100 days in well prepared soil. *C. cumingii* takes about 317 days. Stray



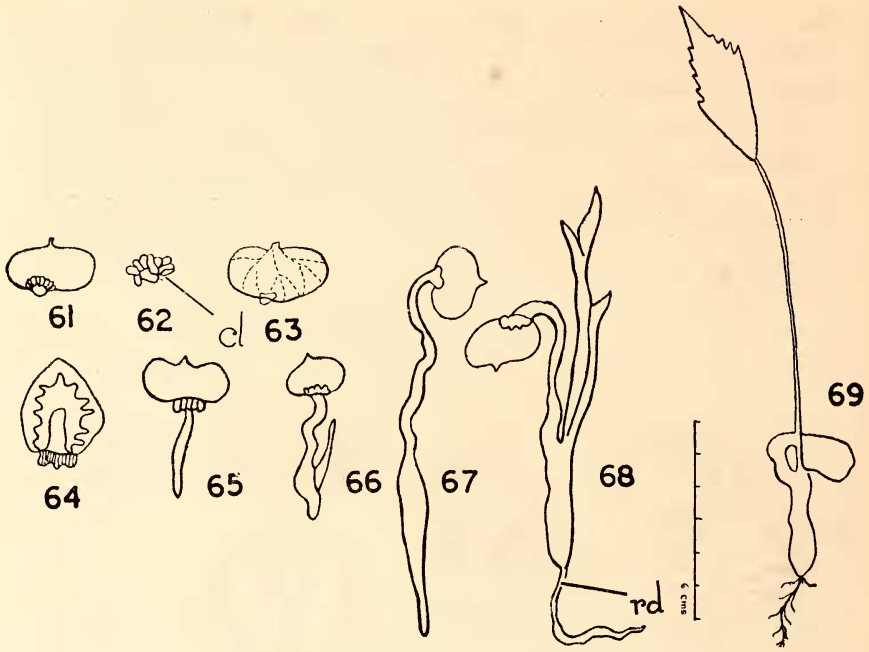
Figs. 55-60. Fruits and seeds of *Caryota*

Fig. 55. *C. urens*. Fig. 56. *C. mitis*. T. S. of fruit-*ep*, epicarp : *mc*, mesocarp ; *en*-endocarp ; sc-seed coat ; rn-ruminations. Fig. 57. *C. urens* : T. S. of seed showing ruminations and endosperm-*en* (diagrammatic). Fig. 58. *C. mitis* : T. S. of seed (diagrammatic). Fig. 59. *C. urens*. Fruit. Fig. 60. *C. maxima*. Fruit

references to the germination of *Caryota* seeds have been made by Gatin (1912) and Saakov (1954) in *C. urens* and *C. sobolifera*. As no detailed account of it, however, was available, it is given below in *C. urens* and *C. rumphiana*.

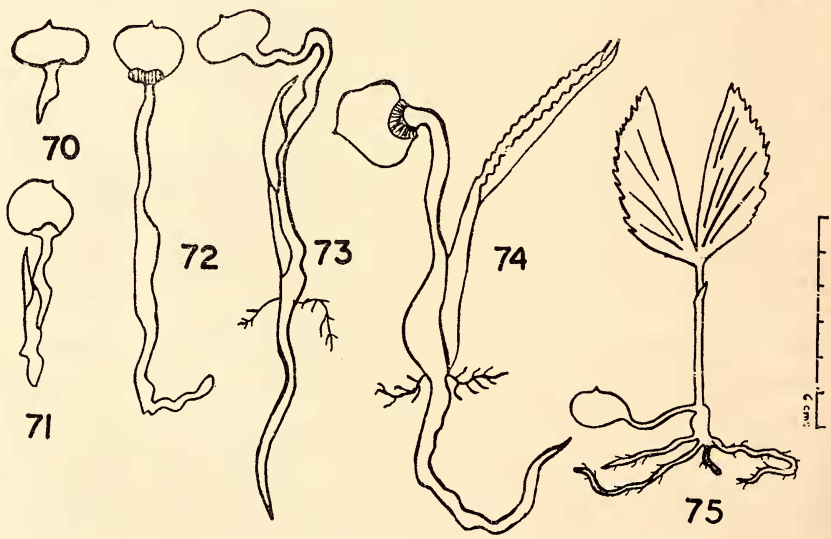
The first plumular leaf appears as a sheathing scaly leaf in *C. urens* and *C. rumphiana*. In both the species, a small protuberance is formed early, through which a cotyledonary tube comes out and forms a frilled collar-like structure around it (Text-figs. 61-62). Its function seems to be absorption. The tube so formed grows vertically downwards and gets swollen in the middle. The swelling enlarges and the plumular initial emerges from it. The radicle goes down and the adventitious roots come out.

The plumular sheath gets split and eophylls begin to unfold. Scaly sheathing leaves appear next. A single simple eophyll emerges and gets split into a bilobed structure. The single eophyll stage is of



Figs. 61-69. Germination of seeds in *Caryota*

Figs. 61-64. *C. urens*. Early stages in germination. Note the Collar-cl in Fig. 62. Fig. 65. A cotyledonary tube emerging through the Collar. Fig. 66-69. Further stages in germination. Note the swelling of the tube in 67, the emergence of plumular initials in 66 and sheathing leaves and the radicle—*rd* in Fig. 68. Fig. 69. A seed ling with simple eophyll



Figs. 70-75. Germination of seeds in *Caryota*

Figs. 70-74. *C. rumphiana*. Germination of seed. (Note the typical remotive type of germination in Fig. 73). Fig. 75. *C. mitis*. A bifid seedling (after Tomlinson 1960)

very short duration and easily escapes attention. When the seedling establishes itself firmly, the seed gets detached from the region of the collar. Early stages of germination in *C. urens* and *C. rumphiana* are similar (*cf.* Text-figs. 61-64, 70-74). According to Saakov (1954) germination in palms is of two types: (1) the *Admotive* type in which the middle piece of coleorrhiza or the germ-tube is very small or absent as in *Cocos* and (2) *Remotive* type in which the middle piece of germ-tube is very long as in *Phoenix* or *Caryota* described here. In most palms, germination is of the *Remotive* type.

B. *Habitat and Distribution*

The genus *Caryota* appears to be of Indo-Malayan origin. Four species are native to India. Besides India, other centres of distribution are Andamans and Nicobar Islands, Indonesia and Philippines (Map). The genus is conspicuously absent in the New World. The number of valid species of *Caryota* is about a dozen according to Blatter (1926) and 13 according to Moore (1960 a).

The Map shows the distribution of palms, and of all the valid species of *Caryota*. They lie within 20° N. and 20° S. *C. urens* has by far the widest geographical distribution. *C. rumphiana* is confined to India and northern Australia and *C. mitis* mainly to Andamans. The remaining species are confined to Malaysia and Philippines where many of them are concentrated.

C. *Past History of the Genus*

Most of the present day species seem to be of recent origin. The only authentic record of it in the past is by Reid & Chandler (1933) who found its seeds in the London Clay Flora, belonging to the Tertiary period. They have described these under the name *Caryotispermum cantiense* which had three seeds, 0·9 cm. in diameter, instead of two as in *C. urens*, or one as in *C. mitis*. Apparently this Tertiary species was three-seeded, though in point of size and shape of its seeds, it agrees with those in *C. urens*. The genus thus seem to have undergone evolutionary changes as shown below:—

3-seeded Tertiary species—*Caryotispermum cantiense*.
2-seeded living species—*C. urens*, *C. maxima*.
1-seeded living species—*C. mitis*.

D. *Systematic Position of the Caryotoideae*

Systematic position of the Caryotoid palms, *Caryota*, *Wallichia*, *Arenga*, and *Didymosperma* has been controversial. Martius (1850)